

TIME-ACTIVITY BUDGET FOR BREEDING GREATER GOLDEN-PLOVERS IN NORWEGIAN MOUNTAINS

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Precocial birds, including shorebirds, are more predisposed toward the evolution of uniparental egg and brood care than are altricial birds, as their chicks usually feed themselves (e.g., Wittenberger and Tilson 1980). In extreme cases, as in polygynous and polyandrous systems, incubation and brood-care may be left entirely to one mate; in species with a "rapid multiclutch system" (Hildén 1975, 1979) the mates care for one brood each. In many monogamous species the brood is sooner or later left in care of one of the parents, often the male (Pitelka et al. 1974).

In the Greater Golden-Plover (*Pluvialis apricaria*) both parents take part in the breeding duties (Nethersole-Thompson and Nethersole-Thompson 1961, Byrkjedal 1978a, Parr 1980), although males may be solely in charge of broods late in the season (Byrkjedal 1978a). Apparently, in the Greater Golden-Plover, cooperation by both mates through most of the season is needed for successfully rearing young. Based on a time-activity study of Greater Golden-Plovers in southern Norway, I analyze the labor division between males and females and discuss why a biparental mating system is maintained.

MATERIAL AND METHODS

Sampling of data.—The data were collected from a Greater Golden-Plover population at 1200–1300 m elevation in the middle alpine zone at Hardangervidda, southern Norway, in the summers of 1979–1981. The study area is described by Byrkjedal (1978a) and Kålås and Byrkjedal (1984a).

The time-activity budget is based on "focal-animal sampling" (Altmann 1974) applied to visual observations and radio-tagged birds. Visual observations were done on six pairs in the prelaying period, two pairs on nest, four off-duty females during the incubation period, and three pairs with chicks between 1 and 11 days old. Radio-tagging was attempted using transmitters (TX142-1S, weighing 3–4 g) emitting a pulsing "beep" signal detectable up to about 1000 m. Transmitters were glued to the back feathers of birds. As transmitters came off with molt, useful data were obtained only from one male in the incubation period and one female after hatching. In addition to the two nests observed visually, nest attendance was monitored in five nests with a Grant thermograph connected by a sub-surface wire to a thermistor pointing up amidst the eggs. The thermograph recorded nest temperatures continually for 3–6 days. The sex of the incubating bird was identified on 58 nest inspections at 16 nests.

Activities recorded visually were alert and non-alert feeding (defined by alert and non-alert stances between pecks) (Fig. 1), standing and running alertly, agonistic behavior (inter- and intraspecific aggressiveness), courtship, running and flying (while not being alert, or

chasing other birds, or feeding), preening, standing inactively (relaxed posture) (Fig. 1), and sleeping. "Alert feeding" took place only in the posthatching period, and in the construction of the time budget half the "alert feeding" time was assigned to "alertness" and half to "feeding." For birds sitting on the nest, I also recorded tossing of nest material into the nest, alertness, freezing, and on and off periods. As assessed through several hours of simultaneously viewing the birds and listening to the radio signal, the radio-tagging allowed me to distinguish (1) flight, (2) running on the ground or preening, (3) staying motionless, or (4) feeding. The frequency of aerial display through the 1981 season was noted during some of the visual observation sessions by recording for each minute whether aerial display (from any bird, not just the one under observation) had occurred.

Finally, feeding methods and pecking rates were recorded, both during time-activity observations, and in separate observation sessions. I distinguished (1) pecking at vegetation (indicated feeding on berries and adult insects [Byrkjedal 1980]), (2) pecking at the ground (indicated feeding on adult insects, especially carabids), and (3) probing in the ground (indicated feeding on larvae and earthworms). Birds were observed for at least 20 min while feeding. Altogether 2372 pecks were classified during a total of 777 min of observations on actively feeding birds. Body condition index ($100 \times \text{weight [g]} / \text{wing length [mm]}$) was obtained from birds shot for stomach analyses in 1974 and 1975 (Byrkjedal 1980) and from birds trapped for banding.

The observed birds were individually recognizable by color bands or characteristic plumage markings, except the four off-duty females. The behavior of these females was studied at the edge of a large bog, where there were no golden-plover territories. A varying number of golden-plovers stayed there during the season, most of them having female-like plumage. The studied birds were considered off-duty females as they were seen to enter the area from the breeding hills at the time of the morning changeover at nests (about 10:00 h), and by their diffuse plumage patterns. For data on plumage patterns in relation to sex and age, see Byrkjedal (1978b), Parr (1980).

The observations were made at 300–600 m, occasionally at a shorter distance, from a blind or a car. A 20–30 \times spotting scope and a tape recorder were used. When possible, data for both mates in pairs were recorded simultaneously; otherwise observation bouts of about 30 min were alternated between male and female. Observations on each pair or single bird were done for several hours in succession. I attempted to cover the daylight hours equally, but did not succeed (Appendix 1), as birds were easily disturbed.

Construction of a time budget.—Time budgets usually change during the day (Maxson and Oring 1980). Accordingly, in constructing a 24-h time budget for the different breeding stages I made the following assumptions: In the prelaying period I estimated two alternative time budgets by assuming (1) that the activity remained the same throughout the 24-h period; and (2) that the birds rested at night. In the incubation period off-duty females rested 3 h in the middle of the day. I lacked evening observations of such females, but I assumed that they engaged in the same activities as in the morning and afternoon. Off-duty male time budget is based on telemetric monitoring. The time not spent feeding was considered as alertness for the time budget estimation, as frequent alarm calls were heard. Just after hatching the females brooded through the night (telemetric monitoring), and I assumed they did so in the first week of the chicks' lives. Males' nighttime and daytime activities after hatching were considered to be the same, as vocalizations by a male were heard during the night from different directions, while I monitored his mate telemetrically. Probably, this somewhat overestimates his guarding activity and underestimates feeding, resting, and preening. When the chicks were 9–11 days old, the parents took a long midday and early afternoon resting period. Early morning and late evening activity frequencies were similar in both sexes, and I assumed the same activities over the night.

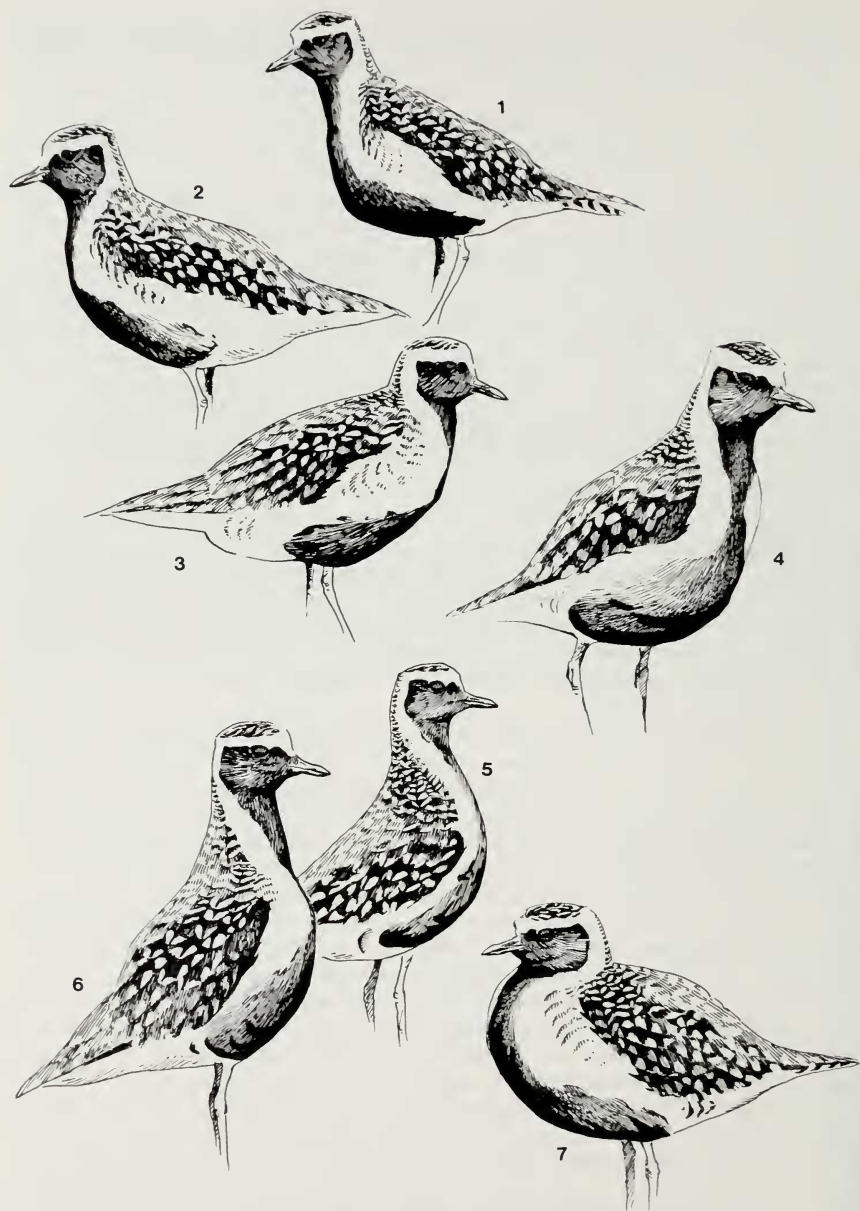


FIG. 1. Postures of Greater Golden-Plovers. 1-4 = non-alert postures, 5-6 = alert postures between pecks, 7 = relaxed posture.

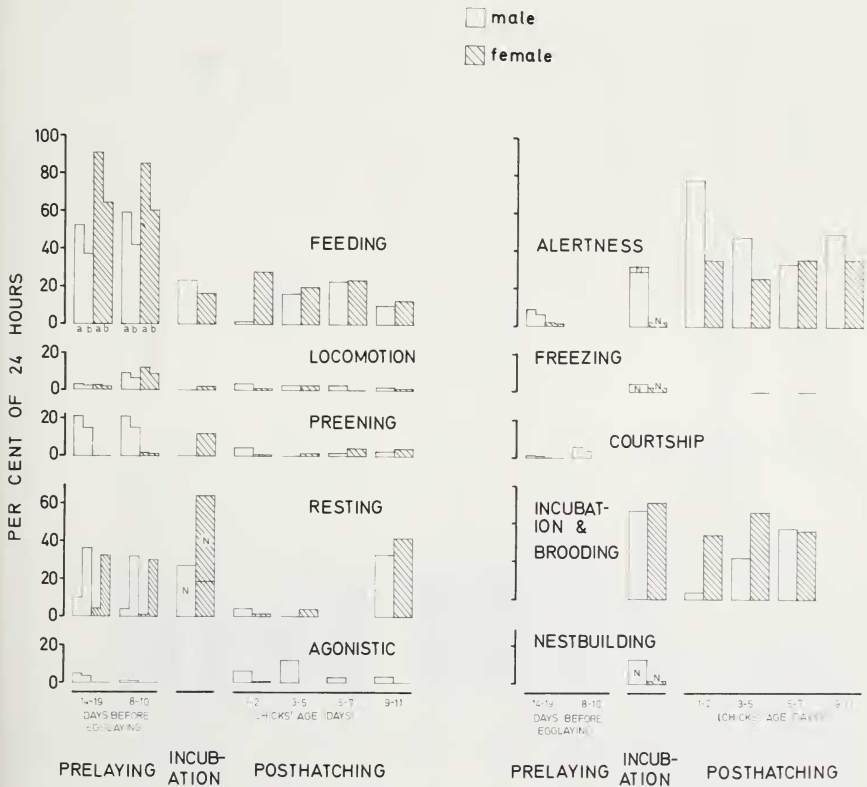


FIG. 2. Estimated frequencies of behavior patterns of Greater Golden-Plovers at different stages of the breeding cycle. Behavior at egg laying and hatching was not sampled. N = behavior performed on nest (all Ns add up to the percentage of time spent incubating). There are two alternatives in the prelaying period: (a) = daytime equals nighttime activities, (b) = nighttime activity (7 h) = resting. "Agonistic" includes both aerial display and chasing of intruders.

RESULTS

Prelying activities.—Both males and females performed all their prelying activities on the territory. The most time-consuming activity for both mates was feeding; in no other part of the breeding period was so much time spent feeding (Fig. 2). Females did little else but feed and rest. Males guarded the territory, stayed alert, performed aerial displays, and chased intruders. Only rarely did females chase away intruders. Usually they stood alert as the male did the chasing.

Although the males apparently found ample time for preening, their

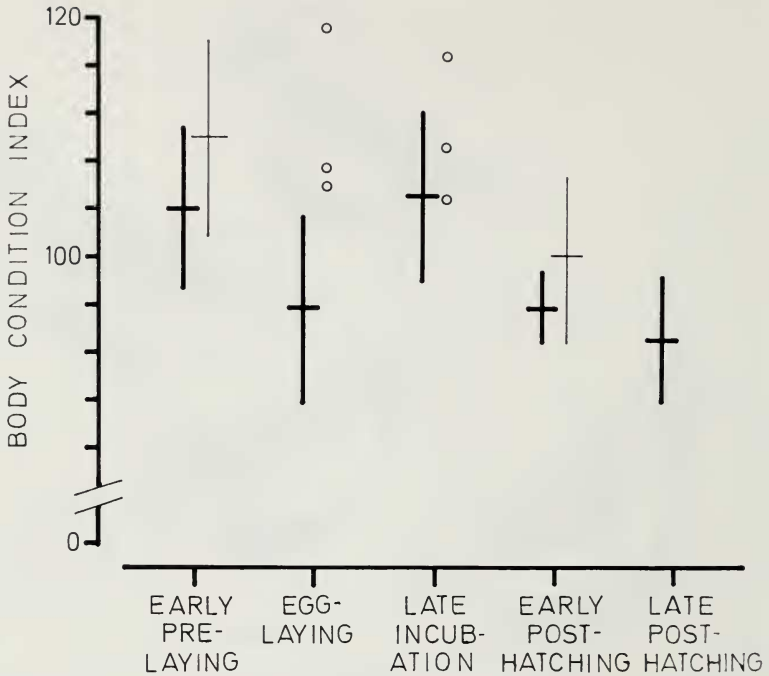


FIG. 3. Mean (\pm SD) body condition indices ($100 \times$ weight [g]/wing length [mm]) of males (thick lines) and females (thin lines) at different stages of the breeding cycle, sampled as follows (several years): Early prelaying: 11–15 May (22 males, 8 females), egg laying: 6–11 June (6 males, 3 females), late incubation: 30 June–10 July (6 males, 3 females), early posthatching: 22 July (9 males, 5 females), late posthatching: 16–18 August (17 males, 0 females). Circles = individual females.

body condition declined from prelaying to egg laying ($t = 2.4475$, $df = 25$, $P < 0.01$) (Fig. 3), indicating a high energy expenditure. During the prelaying period both males and females found most of their food on the surface and in the ground. During uninterrupted feeding bouts the pecking rate was about 2–3 pecks per min (Fig. 4).

Activities during incubation period: on the nest.—The parents shared the incubation duties about equally. The males were relieved on the nest by the females about 10:00 and the females by the males about 22:00 (Fig. 5). Thus, the sitting spells lasted for about 12 h. During incubation duty the incubating bird spent 1–2% of the time off the nest (Table 1). This sometimes coincided with herds of caribou (*Rangifer tarandus*) passing across the nest-site area, and was not considered to be feeding excursions. During a total of 18,054 min of machine recordings and visual observations at seven nests an overall nest attendance of 98.3% was found. (This does not include data from egg-laying or hatching periods.)

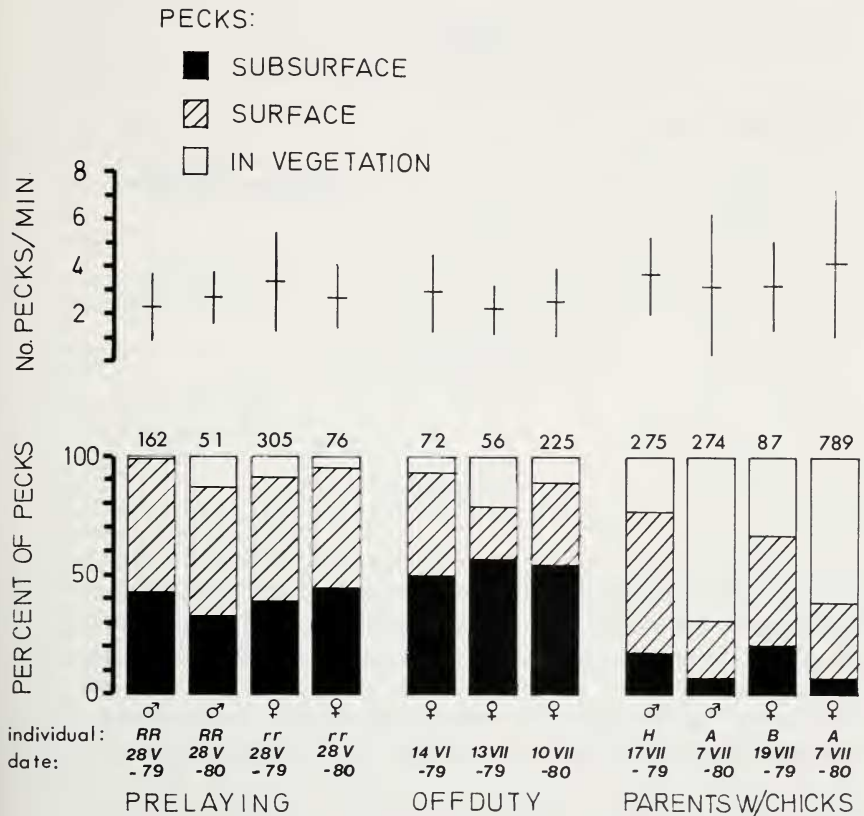


FIG. 4. Pecking rates and frequencies of pecks in the ground, on the surface, and in the vegetation by feeding Greater Golden-Plovers at different stages of the breeding cycle. Sample sizes (number of pecks) are given above the bars.

On the nest males spent about 58% and females 88% of the time relaxed (Fig. 2). The males especially engaged in throwing bits of straw and lichens into the nest. Both were occasionally alert and "froze" (squatted flat) when Common Ravens (*Corvus corax*) or Mew Gulls (*Larus canus*) flew over.

Activities during incubation period: off-duty.—In seven of eight observations of morning changeovers, females left the territories for distant areas where they fed extensively, rested, and preened (Fig. 2). Females were not seen on the territories when the males were incubating.

Observed changeovers (N = 8) in the evening did not reveal whether any of the males left the territories. Males may have been on territories in early morning and late evening when the females incubated, but their behavior was cryptic. From 21:30 to 00:15 on 16 and 17 July 1981, a

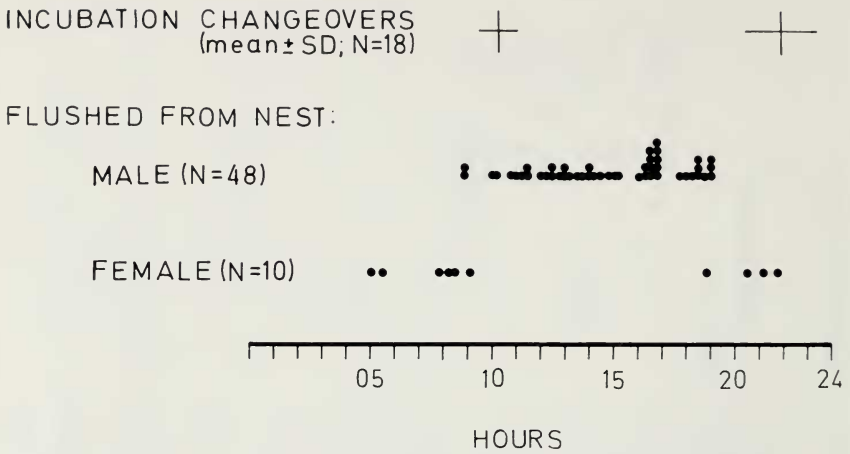


FIG. 5. Changeovers at nest.

radio-tagged male was on his territory, spending 30% of the time feeding, 30% of the time being active but not feeding, and 40% of the time standing still (Fig. 2). He left at 00:16 to feed nonstop, 1 km away, until 02:51, when he returned. Recording was terminated at 03:01; he was then active but not feeding.

Although mates shared the incubation equally, females rested about 62% and preened about 11% of the time, while males spent only 13% and <0.5% of the time in these activities. On the other hand, males were alert 31% of the time (based largely on telemetric recordings) compared to 1.5% of the time by females.

In the latter half of June, when most golden-plovers were on nests, the population showed a peak in the aerial display activity (Fig. 6) that was significantly higher than in the prelaying period ($\chi^2 = 4.9603$, $df = 1$, $P < 0.05$) but not significantly higher than in early posthatching ($\chi^2 = 2.3009$, $df = 1$, NS). I failed to record any such activity of the "focal males" during the incubation period. The radio-tagged male was studied at such a late date that most of the aerial display activities in the population had ceased.

In males, body condition increased significantly from egg laying to late incubation ($t = 2.0922$, $df = 10$, $P < 0.05$) (Fig. 3). The six females I weighed indicated that females also terminated the incubation in good condition (Fig. 3). Two of those weighed at egg laying were collected and had eggs in the oviduct.

The frequencies of pecks of off-duty females in June were similar to those in prelaying pairs in May (Fig. 4). In 1979, off-duty females in July, however, pecked significantly more often at the vegetation ($\chi^2 = 6.604$,

TABLE 1
NEST UNATTENDED, AS RECORDED BY MEANS OF THERMOGRAPHS IN FIVE NESTS^a

	$\bar{x} \pm SD$	Number of registrations
Number of times off nest per sitting spell:		
Male	1.82 \pm 1.54	11 spells
Female	1.00 \pm 1.08	13 spells
Duration of periods off during sitting spells (min):		
Male	10.70 \pm 9.95	23 times
Female	7.19 \pm 9.59	13 times
Duration of nest unattended during changeover (min):		
Morning	1.86 \pm 1.98	12 cases
Evening	3.01 \pm 3.41	17 cases

^a Sitting sex according to data in Fig. 5.

df = 1, $P < 0.01$) and significantly less often on the ground ($\chi^2 = 5.738$, df = 1, $P < 0.02$) than they did in June. The off-duty females in July probed more often ($\chi^2 = 19.91$, df = 1 [1979], $P < 0.001$; $\chi^2 = 271.3$, df = 1 [1980], $P < 0.001$), and pecked less often on the ground ($\chi^2 = 8.873$, df = 1 [1979], $P < 0.01$; $\chi^2 = 1.009$, df = 1 [1980], NS) and on the vegetation ($\chi^2 = 2.361$, df = 1 [1979], NS; $\chi^2 = 180.7$, df = 1 [1980], $P < 0.001$).

Posthatching activities.—Fig. 2 gives the time budget of three pairs representing four sampled stages in the chicks' ages (1–2 days, 3–5 days, 5–7 days, 9–11 days). Observations later in the posthatching period were difficult to obtain, as birds with chicks gradually moved out of view, even when the observer was 300–400 m away.

In the first week after hatching both mates were engaged in guarding and brooding (Fig. 2). Males also engaged in territorial defense. Comfort activities (resting and preening) were reduced by both mates, and during 1–2 days after hatching, the male spent less than 1% of the time feeding. The time spent feeding by the female, however, did not seem to be affected by the presence of the chicks. In the chicks' second week comfort activities were at prelaying levels in male and above incubation level in female, and both mates had reduced the time spent guarding and brooding.

Both parents, when guarding or brooding chicks less than one week old, constantly emitted soft "peep" notes. These calls were impossible to hear beyond 100 m, but they were inferred from slight mandibular and gular movements. Calls did not occur when the chicks were 9–11 days old.

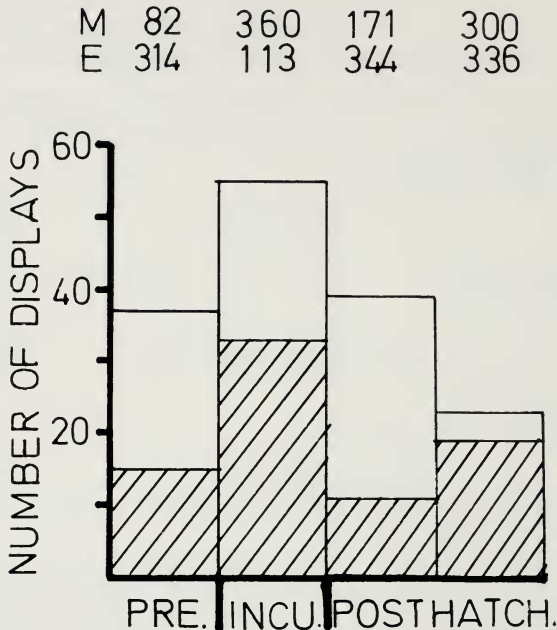


FIG. 6. Estimated number of aerial displays per 5-h morning observations (05:00–10:00, open bars) + 5-h evening observations (15:00–22:00, hatched bars), based on all displays recorded during observation bouts, not only those of focal birds. Observation time (min) is given above the bars (M = morning, E = evening). Data are from 1981; prelaying was sampled 20–22 May, incubation 11–17 June, early posthatching 28 June–7 July, mid-posthatching 8–14 July.

Simultaneously collected data on both mates showed that during the chicks' first week, and especially in their first 2 days, both parents rarely engaged in nonattentive activities before the other one had assumed guarding duties for a couple of minutes (except in 2 cases of 197 changes of activity). When the chicks were 9–11 days old, both mates most often engaged in nonattentive as well as attentive activities simultaneously (Fig. 7).

Even newly hatched broods were very mobile, and during the first few days broods were clearly far beyond the original nesting territory. Nevertheless, the male defended a large area around the brood. Attacks on conspecifics were elicited from about 100 m. On a few occasions the female took part in chasing as well. Both parents fed near the brood, except that a female, after having brooded without interruption for 5 h 25 min during the night, left for a 17-min feeding exodus (telemetric monitoring). During this feeding bout the male immediately took over the brooding and otherwise stayed close to the chicks.

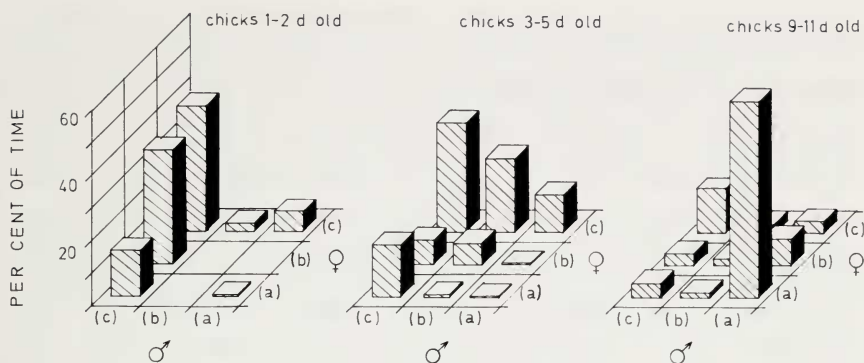


FIG. 7. Simultaneously recorded activities of mates at different posthatching stages. (a) = nonattentive behavior (feeding non-alertly, preening, resting, running, flying, aerial display, chasing), (b) = semiattentive behavior (alert feeding), (c) = attentive behavior (standing or running alertly, brooding). Left to right: Pair 6/81 28–29 June (345 min observations), pair 10/81 2–4 July (532 min observations), pair 6/81 8–10 July (529 min observations).

In males, body condition declined significantly in the course of the first week after hatching ($t = 3.4222$, $df = 13$, $P < 0.001$), but only slightly during the remainder of the posthatching period ($t = 1.1836$, $df = 24$, NS) (Fig. 3). In females, there might also have been a tendency for a rapid decline in body condition after hatching, as their body condition at that time was below that of early prelaying ($t = 2.1828$, $df = 11$, $P < 0.05$) (Fig. 3).

Parents with chicks found most of their food on the ground and in the vegetation, in contrast to prelaying pairs and off-duty females, which found their food chiefly on and beneath the ground surface (Fig. 4). Parents with chicks seemed to have a slightly, but not significantly ($t = 0.2500$, $df = 200$; $t = 0.2578$, $df = 279$), higher pecking rate than at other times.

DISCUSSION

Biparental care can improve (1) incubation efficiency, (2) nest and brood survival, and (3) mate condition to the extent it is important for reproductive success (Oring 1982). Here I discuss how biparental care in the Greater Golden-Plover affects these aspects.

Shared incubation enables the nest to be covered almost all the time. The high incubation constancy found in Greater Golden-Plovers is similar to that found in other shorebirds with shared incubation; in uniparental incubation the constancy is usually below 90% (Norton 1972, Ashkenazie and Safriel 1979, Maxson and Oring 1980, Kondrat'ev 1982, Löfaldli 1985). Low incubation constancy may increase incubation period (Pien-

kowski 1984) and thereby the risk of nest predation, but shorebird embryos may be quite tolerant to disruptions of egg-warming (Myhre and Steen 1979). In uniparental incubation there is more traffic to and from the nest than in biparental incubation (Norton 1972, Kondrat'ev 1982, Löfaldli 1985), as conflicts between needs for self-maintenance and egg-warming select for many short feeding recesses, rather than few and long ones (Löfaldli 1985). In Greater Golden-Plovers there are about 120 passings to and from a nest during the incubation period, whereas in uniparental Eurasian Dotterels (*Charadrius morinellus*) breeding in the same area there are about 1400 (estimated from Wilkie 1981). Such traffic could make the nest more detectable to predators (Pienkowski 1984).

Shared incubation allows the golden-plovers time to seek good feeding sites far from their territories. The females' exoduses lasting almost all their off-duty time and the males' cryptic behavior when on territories while females incubate make Greater Golden-Plovers very unobtrusive during the incubation period (Kålås and Byrkjedal 1984b), which is apparently a part of their antipredator strategies. Although they perform distraction displays when flushed from the nest, they never chase predators by "dive-bombing" as do Black-bellied Plovers (*Pluvialis squatarola*) and Lesser Golden-Plovers (*P. dominica*) (Ratcliffe 1976; Sordahl 1981; Kondrat'ev 1982; Byrkjedal, unpubl.).

Close cooperation by the parents during the first week after hatching, when at least one of them is attentive at all times, is probably an efficient way to guard chicks. The time-activity budget and body-condition index show that tending in the early chick phase is very intense, while after 1½ weeks the parents are more relaxed and do not take turns to monitor the chicks continually. A similar change in development of parental care in the course of the posthatching period has been found in the biparental Killdeer (*Charadrius vociferus*) (Lenington 1980), some lapwings (Walters 1982), and Semipalmated Sandpipers (*Calidris pusilla*) (Ashkenazie and Safriel 1979), and may be common in shorebirds with biparental care. The behavioral change supports the idea that small chicks respond less rapidly to alarm calls, are more likely to go astray, and are less able to find good feeding patches than later on when they are more experienced (Lenington 1980, Walters 1982). Spotted Sandpiper (*Actitis macularia*), Killdeer, and Black-tailed Godwit (*Limosa limosa*) adults tending alone fed near normal levels, at the cost of constant chick surveillance (Maxson and Oring 1980, Lenington 1980, Byrkjedal 1985).

Weight loss during breeding in birds is common, and is usually considered indicative of a negative energy balance (e.g., Hussell 1972, Askenmo 1977, but see Norberg 1981 for a different view). In the Greater Golden-Plover the body condition index shows that incubation is an

energetically relaxed period, enabling the birds to regain physically from expenditures of territorial behavior, courtship, and egg laying, and to put on weight before the energetically demanding early posthatching period. Although Ashkenazie and Safriel (1979) considered incubation to be energetically costly for Semipalmated Sandpipers, their weights for incubating males, as well as weights for Dunlins (*Calidris alpina*) and Eurasian Oystercatchers (*Haematopus ostralegus*), indicate that in biparental incubation this may not be so (Holmes 1966, Mercer 1968, Soikkeli 1974). Even Spotted Sandpiper males incubating alone often gain weight, but their food situation is usually extremely favorable (Maxson and Oring 1980). Male Eurasian Dotterels in the same area as the present study lost weight when they incubated alone (Kålås and Byrkjedal 1984a); so weight gain in the incubating golden-plovers in spite of active molt over most of the incubation period (Byrkjedal 1978a) apparently was facilitated by shared incubation. Not only could individual golden-plovers seek good feeding spots far away, but they also had time to concentrate on favorable (subterranean) prey (see Byrkjedal 1980 for details on food). I suggest that holding of large territories in Greater Golden-Plovers (Nethersole-Thompson and Nethersole-Thompson 1961, Ratcliffe 1976, Parr 1980, Edwards 1982) and the intense early posthatching chick care would not be feasible without the energetic advantage from shared incubation.

Golden-plover territories apparently function chiefly to decrease nest and brood predation, as spacing prevails into the chick period, while feeding inside the territory takes place chiefly in the prelaying period. I have found a positive relationship between spacing and nest survival in this golden-plover population (Byrkjedal, unpubl.). Decreased nest predation with spacing of nests has also been documented for Snowy Plovers (*Charadrius alexandrinus*) (Page et al. 1983).

Why is it necessary for Greater Golden-Plovers to have large territories and highly intense chick care whereas the Eurasian Dotterel reproduces successfully in the same area and habitat and on the same food resources without these features? Maynard Smith (1977) presents a model showing how biparental care is selected for when it gives higher reproductive outcome than uniparental care of multiple clutches, and the chances for multiple matings are low. The difference between uniparental and biparental care is probably greater in golden-plovers than it would be in dotterels, as larger body size and four large vs three small eggs seem to make the former more detectable to predators (Byrkjedal, unpubl.). In the present study area, dotterels lose about 48% of the nests to predators (Kålås and Byrkjedal 1984a) compared to 78% in golden-plovers (Byrkjedal, unpubl.). Maxson and Oring (1980) considered that a high rate of nest predation could select for female emancipation in shorebirds, en-

hancing rapid replacement clutches, but as a prerequisite, one mate must be almost as good as two in caring for eggs and chicks (Maynard Smith 1977, Oring 1982). In Greater Golden-Plovers the prospects for successful uniparental care are probably very low, as four widowed females deserted their nests in less than 50 h after the loss of their mates.

SUMMARY

The time-activity budget of the Greater Golden-Plover (*Pluvialis apricaria*) was studied on a middle alpine breeding ground in southern Norway by means of visual focal-animal sampling, radio-tagging, and automatic incubation recorders. Body condition indices were obtained from shot and trapped birds.

Territory defense is mainly a male task. Large territories are maintained through the incubation period, and a similar-sized area around the brood is defended, although the brood leaves the nesting territory. By sharing the incubation (12 h daytime sitting spells in males, 12 h nighttime sitting spells in females) the birds feed extensively and improve their physical condition. This enables them to put maximum effort into periods of high energetic demands like prelaying territorial guarding, egg laying, and early posthatching guarding of chicks. Besides, off-duty exoduses from the nest area greatly facilitate unobtrusiveness during the incubation period. Close parental cooperation ensured constant guarding of newly hatched chicks; the intensity of chick-guarding declined in the course of 1½ weeks after hatching. It is suggested that biparental care in Greater Golden-Plovers is needed to cope with nest and chick predation.

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APPENDIX 1
DISTRIBUTION OF OBSERVATION TIME (MIN)^a

Category of bird	Date	Sex	Hours ^b				Obs. time (bird min)
			00:01-06:00	06:01-12:00	12:01-18:00	18:01-24:00	
Prelaying:							
3 pairs	28 May 1980	M	18	111	97	0	226
		F	0	80	113	0	193
3 pairs	19-22 May 1981	M	24	220	313	256	813
		F	24	220	262	258	764
Incubation:							
Off-duty							
1 bird	17-18 Jul. 1981	M	180 ^c	0	— ^d	150 ^c	330 ^c
4 birds	10 Jul. 1980	F	— ^d	436	952	0	1388
On nest							
2 nests	11-17 Jun. 1981	M	— ^d	88	122	26	236
		F	17	293	— ^d	7	317
5 nests ^e	10 Jun.-8 Jul. 1981	M + F	4533	4235	4235	4498	17,501
Posthatching:							
Chicks' age (days)							
1-2 (Pair 6/81)	28-29 Jun. 1981	M	0	95	232	136	463
		F	0	81	251	62	364
3-5 (Pair 10/81)	2-4 Jul. 1981	M	30	101	254	192	581
		F	10 + 311 ^c	88	319	184 + 223 ^c	601 + 534 ^c
5-7 (Pair A/80)	7-9 Jul. 1980	M	15	146	142	81	384
		F	26	163	203	17	409
9-11 (Pair 6/81)	8-10 Jul. 1981	M	20	146	273	216	655
		F	43	109	276	205	633

^a Excluding time when birds were temporarily out of sight during observation bouts.^b Sunrise and sunset in the period 19 May-18 July were at 03:51-03:44 and 21:22-21:45, respectively.^c Monitored by radio telemetry.^d All incubation or off-duty in that period by the other mate.^e Monitored by thermograph.